The University of Chicago

TUSSOCK MEADOWS IN SOUTH-EASTERN WISCONSIN

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL
SCIENCES IN CANDIDACY FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY
1934

By
DAVID FRANCIS COSTELLO

Private Edition, Distributed by
THE UNIVERSITY OF CHICAGO LIBRARIES
CHICAGO, ILLINOIS

Reprinted from
The Botanical Gazette
Vol. 97, No. 3, 1936

The University of Chicago

TUSSOCK MEADOWS IN SOUTH-EASTERN WISCONSIN

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL
SCIENCES IN CANDIDACY FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY
1934

By
DAVID FRANCIS COSTELLO

R. UNIV.
BIBLIOTHEEK
LEIDEN

Private Edition, Distributed by
THE UNIVERSITY OF CHICAGO LIBRARIES
CHICAGO, ILLINOIS

Reprinted from
The Botanical Gazette
Vol. 97, No. 3, 1936

TUSSOCK MEADOWS IN SOUTHEASTERN WISCONSIN

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 468

DAVID F. COSTELLO

(WITH NINE FIGURES)

Introduction

Throughout eastern Wisconsin, and extending eastward to the Atlantic seaboard, is a type of sedge meadow which seems to have been little studied and scarcely mentioned in the literature. It is characterized by numerous tussocks (figs. 1, 3), formed by sedges with the caespitose habit, which reach a height of 1–3 feet and which are separated by passages 1–4 feet wide. In bluegrass pastures the remnants of these tussocks are frequently represented by grass covered mounds a few inches in height. They almost invariably attract the attention of the traveler entering the region for the first time, but are taken for granted by the inhabitants, who usually explain their presence as being due to the trampling of livestock.

Although the floristic composition and the gross environment of these tussock meadows are fairly well known, ecological studies concerning the tussock habit, the floristic structure of the tussock association, and the factors which accompany and influence the initiation, development to maturity, and subsidence of these communities have been neglected. DRUDE (2) has briefly characterized similar associations in Hungary and has mentioned the gradual replacement of tussock meadows by grassland. WARMING and GRAEBNER (11) mention the formation of tussocks by *Carex paniculata* and *C. stricta* in Europe, and discuss at length the tussock vegetation of the subantarctic islands. They state that "tussock" signifies in general a vegetation of thick, high, bushlike tufts of grasses or grasslike plants. These tufts, composed principally of leaves, surmount compact pedestals which are formed from dead stems and leaf débris and which are ramified by numerous rhizomes and roots. The old pedestals frequently serve as substrata for other plants. NICHOLS

(6) states that the tussock sedge, *Carex stricta*, is "by far the commonest, and ecologically the most important, sedge of Connecticut swamps." He mentions its place in the usual swamp succession, lists a number of species characteristic of the sedge stage, calls attention to the composite habitat afforded by tussock meadows, and notes that the duration of the sedge stage may be long or short. In Wisconsin, STOUT (9) has studied the tussocks formed by *Carex stricta* in

FIG. 1.—*Carex stricta* tussock showing pedestal and tuft of leaves; *Ranunculus delphinifolius* on the ground.

connection with the other vegetation in a wild hay meadow. He gives statistical data concerning the frequence and abundance of the various species, but his work appears to deal with a mixed community rather than with a relatively pure stand of the tussock sedge. He describes the stooling habit of this sedge, discusses briefly its growth form and adaptations, and points out that the exclusiveness of *Carex stricta* is a problem that needs further study. In the introduction to his paper he includes a summary of the literature dealing with the geographic distribution of meadows and the classi-

fication of low moist formations. Although his paper does not deal primarily with the ecology of *Carex stricta*, it contains the best existing discussion of the species that has been written to date.

The present paper deals with the ecology of the tussock sedge, the structure of the tussock association, the place of the association in succession, and the environmental and biotic factors which accompany and influence the association throughout its life history.

The area included in this study comprises most of Ozaukee, Washington, Waukesha, Milwaukee, and Racine counties in Wisconsin. General observations were made of most of the meadow associations in this region within a radius of 35 miles from the city of Milwaukee. An area was selected for detailed study near the southern boundary of Ozaukee County, about 2 miles south of Cedarburg, on the west side of State Highway 57. The strip of meadow studied is somewhat over a quarter of a mile long and an eighth of a mile wide. The east side is low and moist, and consists principally of tussock meadow through which a small stream meanders. The west side rises gradually toward the top of a high ridge. Half way up this ridge, where the soil is kept moist by numerous springs, the tussock meadow again appears. Three-fourths of a mile northwest of this area an ephemeral pond with its surrounding tussock meadows was selected for further detailed study. Both of these areas are typical of scores of others that may be found within the same region.

Observations, beginning in 1927, were made over a period of six years. Detailed work was done in the field during the summers of 1929, 1932, and 1933. Studies of the growth habit of the tussock sedge were made during the winter as well as the summer.

Topographic and physiographic features

The areas considered in this paper all lie within the glaciated region of eastern Wisconsin. Consequently the topography is youthful, the relief is moderate, and the country is gently rolling. The topography is controlled by the Niagara cuesta (5), which is also spoken of as the eastern upland. The upland is underlain by Niagara limestone which dips eastward toward Lake Michigan. Covering the rock is a mantle of glacial drift of variable thickness, consisting principally of till, sand, gravel, and clay. In Waukesha and Wash-

ington counties the Kettle Moraine, an interlobate deposit, is characterized by greater irregularity and by pits or undrained depressions.

Temporary lakes and swampy tracts are common throughout the district. Many of these swampy areas are the result of filling of lakes; others are the result of seepage and poor drainage. According to WHITBECK (14), "Between twelve and fifteen per cent of this area is covered with lakes, swamps, or land that has been swampy." He also states that "not all of the present swamps were former lakes; probably the majority of them have been swamps from their beginnings." It is in these areas and in the drained depressions of the Kettle Moraine that tussock meadows have developed.

Methods

Floristic composition was studied by means of meter quadrats. Quadrats of this size were deemed necessary because of the uneven distribution of the vegetation. Transition areas and tension zones were studied by means of belt transects 0.5 and 1 m. wide. Immature plants were marked by stakes and later identified when flowers or fruit appeared. Doubtful plants were carefully pressed and later checked with authentic herbarium specimens. The presence and number of individuals and the coverage and height of each species within the quadrats were recorded. In order to facilitate counting, the plants were clipped from each quadrat. The culms of grasses and sedges were counted as individuals. Small plants such as *Eleocharis palustris* and *E. acicularis* were not counted but were rated for coverage and height.

In the study of the subterranean plant organs, trenches were dug to a depth greater than that of the deepest roots and the soil was then dissected away from the underground parts with an icepick or other sharp instrument. For more detailed studies of the roots in tussocks the whole pedestal was dug up and transported to the laboratory for dissection. Counts of the roots were made in winter when the frozen pedestal could easily be chopped off with an ax. For purposes of propagation, pieces of tussocks containing both roots and buds were brought into the greenhouse in winter and planted in soil or in water cultures.

Soil samples for moisture determination were taken weekly at depths of 6, 12, and 18 inches. The percentage of moisture was calculated on the basis of the dry weight of the soil.

Evaporation readings were taken from standardized porous porcelain atmometers. The usual precautions concerning rain absorption, the entrance of rain or dew into the bottles, and standardization of the bulbs were observed.

The level of the water table was determined throughout the growing season by weekly readings taken from numerous wells in typical parts of the area. These wells were plugged to reduce evaporation and to prevent seepage from rains or the accumulation of débris from the surface. At frequent intervals they were cleaned and then left undisturbed for at least 24 hours before a reading was taken.

The hydrogen ion concentration of the soil was determined in the field by means of the Morgan soil tester. These readings were checked in the laboratory on dried soil samples with the quinhydrone apparatus.

Vegetation of tussock meadow

Well developed tussock meadows are always dominated by a single species, *Carex stricta*. This plant frequently comprises more than 90 per cent of the vegetation and controls the physiognomy both in summer and in winter. In summer the deep green leaves obscure the pedestals beneath, but the presence of the tussocks is made apparent by the undulating nature of the sedge cover (fig. 2). In winter the hummocky nature of the area is most apparent (fig. 3). The dead leaves and culms, beaten down by wind and rain, form a close thatch about each pedestal.

It is only during the growing season that secondary species are at all conspicuous in the tussock association. In early spring these are apparent because of their showy flowers and the delayed development of the tussock sedge. The summer and autumn species are visible only because they surmount the general level of the meadow. Other species remain secluded beneath the sedge cover and are found only by pushing aside the tufts of leaves that grow from the tussocks.

Ecology of tussock sedge

Initiation and growth of tussocks.—New tussocks are initiated by rhizomes which grow down over the edge of the pedestal in the protection of the thatch of dead leaves, when the tussock is in the water, or which grow horizontally just beneath the soil when

Figs. 2, 3.—Fig. 2 (above), summer aspect of *Carex stricta* association; *Eupatorium* in foreground, *Typha* in background. Fig. 3 (below), well developed tussock association; water table about 4 inches below ground level.

the base of the tussock is a mere rounded hillock in drier situations. The pointed terminal buds of these rhizomes turn upward, producing a tuft of leaves, while roots develop from the base of the bud just beneath the soil. Under the most favorable conditions new tussocks are initiated in water that varies in depth from 6 to 12 inches. In a comparatively short time the leaves and culms appear above the

surface and act as a trap for floating débris, initiating the tussock almost as soon as the leaves appear.

New leaves appearing at the base of the young tuft throughout the growing season result in a well developed clump by the end of summer. Within a few years a pedestal consisting of dried culms, woody stems, old rhizomes, roots, soil, and vegetable matter is built up. Eventually the pedestals rise above the surface of the water (fig. 4), or during dry seasons they stand high and dry (fig. 1). In time

FIG. 4.—*Carex stricta* tussocks invading a pond

the mass of material which supports the clump of leaves becomes a network of fine fibrous roots which grow from the bases of the culms or develop as branches of larger wirelike roots that grow downward into the muck (fig. 9). From the crown of dead leaves above, long pointed buds grow out to produce new foliage each year.

If undisturbed, a tussock for several seasons may consist of a single plant. The culms and rootstocks remain so closely attached that they are dissected with difficulty. Eventually decay of the old woody parts below the surface may separate the stems, with the result that the tussock becomes a mass of interwoven but distinct individuals.

The age to which tussocks may attain is problematical. There is little doubt that under normal conditions they grow and develop for many years. Tussocks initiated in 1928 at the station south of

Cedarburg were 4 or 5 inches in diameter in 1934, but obviously these tussocks were then immature. Occasionally a vertical section through a tussock will show indications of layers of leaf bases and old stems that are deposited yearly. Calculations made on this basis would indicate an age of 40–60 years for some of the largest tussocks. Disregarding their destruction by violent means, by flooding, or by changes in the habitat, there is reason to believe that they may persist for half a century at least.

The rate of growth of larger tussocks is slow. Specimens marked for special study in permanent quadrats have shown almost no change in height or diameter over a period of 6 years. The maximum size to which they may ultimately attain depends upon the conditions under which the sedge grows. At the edges of ponds pedestals 2 feet in height with a diameter of 18 inches are not uncommon. From this size they grade down to small rounded mounds 2 inches in height and 6 inches in diameter.

The percentage of area covered by the bases of tussocks and the number of tussocks per unit area in different habitats are shown in table I. No correlation can be drawn between the percentage of area covered and the size of the tussock. The number of stools per unit area depends upon a great many factors, including the stage of development of the association, the degree of soil saturation, artificial drainage, annual fires, and grazing. In general, the larger the stools the smaller will be their number in a given area.

Vegetative structures of tussock sedge.—The ability of *Carex stricta* to occupy certain areas in almost pure stands depends to a considerable extent upon the habits of the vegetative structures. Plants which at first appear to compete with the tussock sedge may be shown, by an investigation of root and rhizome habits, and of stratification above ground, to be adapted to different environments. The vegetative habits of *C. stricta* seem to offer at least a partial solution to this problem.

Root system.—Two types of roots are present: long, cylindrical, wirelike soil roots which grow straight down into the substratum and slender, tortuous, much branched, fibrous roots which permeate the earthy pedestal of the tussock. The soil roots arise from the sides of the culms or from the short compressed internodal regions

of the woody stem which lie just beneath the surface of the tussock (fig. 9). They are of rather uniform diameter, varying from 2 mm. in thickness at the point of origin to 0.5 mm. a short distance back from the tip. They range in length from 1.5 to 7 dm., depending upon the nature of the substratum, compactness of the soil, water table, and moisture content of the soil. Within the pedestal, especially when aeration is good, they may branch freely, with the result that a matted spongy mass is formed. Below the general soil level branching is less pronounced. This is especially apparent in winter when

TABLE I

COMPARISON OF SIZE AND NUMBER OF TUSSOCKS, AND PERCENTAGE OF AREA COVERED BY THEIR BASES

HABITAT	AV. DIAMETER OF TUSSOCK (DM.)	NO. OF DIAMETER QUADRATS	AV. NO. OF TUSSOCKS PER SQ. METER	PERCENTAGE AREA COVERED BY TUSSOCK BASES
Permanent pond	3.0	64	1.5	10.6
Intermittent pond	3.2	43	2.3	18.5
Morainic depression	3.5	55	1.9	18.2
Floodplain	3.0	80	3.6	25.4
Springy hillside	3.1	35	4.1	10.9
Margin of stream	4.5	32	1.6	15.9
Pond margin	3.6	28	4.2	42.7
Floodplain (burned)	1.5	40	5.0	8.8
Swale	5.0	100	0.9	17.6

the frozen hummock is chopped or broken off; the soil roots then project from the exposed surface like so many stiff wires.

The number of vertical soil roots within the pedestal is considerable. A cross section of a pedestal 1.5 dm. in diameter will show from 250 to 400 roots; larger tussocks will show a correspondingly greater number. The largest tussock examined was slightly over 8 dm. in diameter and showed approximately 3200 roots.

The depth to which the soil roots will penetrate is determined to a considerable extent by the ground-water level. In areas where the water stands continuously above the soil the root system is shallow. If the water table is fluctuating the roots may penetrate to the lowest level of the water table, a distance seldom more than 24 inches below the soil surface.

Root hairs are produced to a limited extent by the periodically submerged soil roots. If the soil is compact and clayey they may be entirely absent. Root hairs are produced in great abundance by soil roots, however, which frequently grow down the sides of the pedestal or which become exposed to the air by the lowering of the water in ponds. A thick feltlike covering is formed by the numerous hairs, which gradually lignify and turn brown. In the greenhouse they may be produced on plants grown in water culture by gradually lowering the water level, or by growing the plants in well aerated soil which is watered sparingly. Whether or not these root hairs possess any power of absorbing moisture from the air has not been determined.

Rhizome system.—Vegetative propagation of *Carex stricta* is accomplished by means of rhizomes. The rootstocks arise from the bases of the culms, and as Stout (9) has pointed out, are of two types: the ascending and the creeping.

The terminal buds of the ascending rhizomes immediately give rise to new leafy shoots and thus increase the height and lateral spread of the tussock. The creeping rhizomes extend a few inches beneath the soil until they reach a length of a foot or more. The terminal bud may then turn upward to produce a shoot and initiate a tussock. Frequently the rhizomes of tall tussocks are bent over the edge of the pedestal, half concealed in the thatch of dead leaves, their long pointed buds directed toward the ground (fig. 9). Occasionally they grow downward through the mass of roots and then horizontally a short distance below the surface of the soil.

Carex stricta is not so strongly stoloniferous as *C. strictior*, which grows in somewhat similar situations and occasionally with the tussock sedge. *C. strictior*, however, does not produce distinctive tussocks but forms large flat clumps. Although the two species are sometimes distinguished with difficulty in herbaria, there can be no doubt of their identity in the field. Mackenzie (4) has pointed out the taxonomic features of these two sedges, including the nature of the stolons.

While the ascending stolons provide both for leaf and flower production, it is apparent that the tussock sedge depends almost exclusively upon vegetative growth for its maintenance. Examination

of thousands of tussocks over a period of more than six years in the Milwaukee region has yielded comparatively few fruiting specimens. Seedlings of *Carex stricta* were never found during this period.

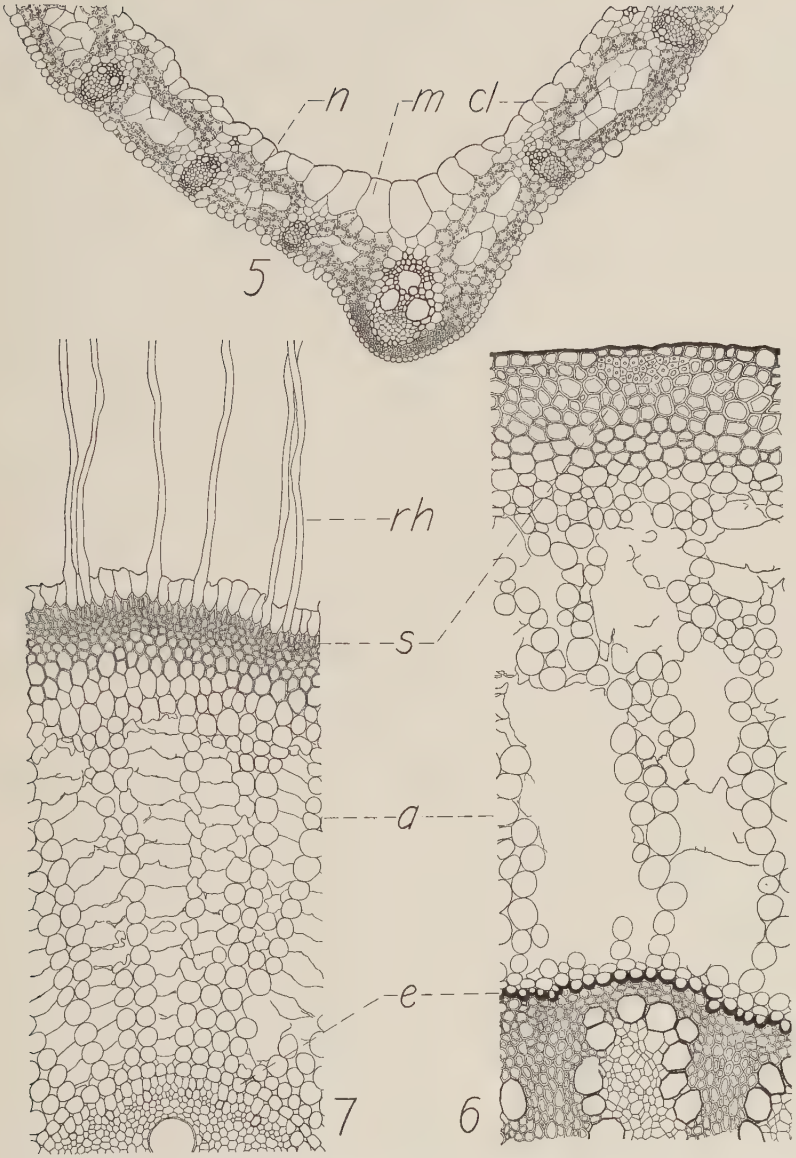
The leaves form a close fascicle as they arise from the ascending stolon; hence in the quadrat studies leaf clusters or culms were counted rather than individual leaves. A tussock 10 inches in diameter will ordinarily show from 100 to 150 clusters. When fully mature the leaves form a dense cover, shading even the open spaces between the tussocks. In early summer the aspect is that of a luxuriant meadow, all evidence of the uneven nature of the ground frequently being obscured.

ECOLOGICAL ANATOMY.—The leaves of *Carex stricta* present a comparatively small area of exposed surface. Although they vary in length from 4 dm. to more than 1 m., they are seldom more than 7 or 8 mm. wide and are usually dried at the tips. When subjected to drought they fold upward on the midrib, but the blades are stiff enough to resist twisting by the wind.

In cross section the leaf is seen to consist of a series of parallel bundles separated by compartments of chlorenchyma (fig. 5). The bundles are surrounded by sclerenchymatous sheaths which are in turn surrounded by non-chlorophyll bearing parenchymatous cells. The chlorenchyma usually surrounds a group of non-chlorophyll bearing cells. In older leaves the latter may break down to form lacunae. The upper and lower epidermis possesses a cuticle of medium thickness. Bulliform or motor cells occur in the groove of the ventral (adaxial) side of the leaf. They provide for the folding of the leaf by their collapse during periods of desiccation.

The leaves of *Carex stricta* are well adapted to withstand high evaporation and the periods of summer drought to which they are sometimes subjected, although they do not show the pronounced xeromorphic structure which is characteristic of some of the upland species of grasses (13). The persistence of the tussock sedge in dry, well grazed pastures may be explained in part by its semi-xeromorphic leaf structure.

The roots and rhizomes show both hydromorphic and xeromorphic structure. HAYDEN (3) has pointed out that the primary indicators of water relations in underground organs are the relative proportions



FIGS. 5–7.—Transverse sections of leaf, rhizome, and root of *Carex stricta* showing ecological anatomy: fig. 5, transection of leaf (*cl*, chlorenchyma; *m*, motor cells; *n*, non-chlorophyll bearing cells); fig. 6, transection of mature rhizome; fig. 7, transection of young root (*e*, endodermis; *a*, aerenchyma; *s*, sclerenchyma; *rh*, root hairs).

of parenchyma, mechanical tissue, and conductive tissue. Xeric structure is indicated by the prominence of the latter two, and the reverse condition is indicated by the first.

In the rootstock (fig. 6) the cortical tissue occupies two-thirds of the radius of the rhizome. The thick walled epidermis surrounds a sclerenchyma layer which is six to eight cells in thickness. The zone of aerenchyma is pronounced and is characterized by large lacunae. A prominent endodermis with thickened radial and inner tangential walls is present. The stele is a close fascicle of numerous bundles, each surrounded by a compact sheath, inclosing a small pith cylinder of thin walled aerenchyma.

In the root (fig. 7) the cortical area represents from two-thirds to three-fourths the diameter of the entire structure. Numerous lignified root hairs may or may not be present. The sclerenchyma layer beneath varies from five to eight cells in thickness. Aerenchyma is even more pronounced here than in the rhizome. The radial and inner tangential walls of the endodermis are strongly thickened. The stele is composed of a single row of bundles surrounding a pith cylinder of lignified cells.

The prominence of mechanical tissue in both the root and the rhizome would seem to indicate xerophytism, while the abundance of aerenchyma indicates hydric tendencies. This condition, however, does not appear to be anomalous when the water relations of *Carex stricta* are considered. As a rule both roots and rhizomes are exposed to the atmosphere for a portion of each growing season. Adequate protection from desiccation is afforded by a sclerenchyma layer in the outer part of the cortex. At other times the root and rhizome systems are submerged. The utility of an aerating system then becomes apparent. The presence of additional mechanical tissue in the stele explains to some extent the difficulty with which tussocks are uprooted or toppled over, either by artificial means or as the result of natural forces.

Tussock association

The vegetation of the tussock meadow is almost exclusively herbaceous. *Carex stricta* is the dominant of the association. Other sedges occur, particularly *C. bebbii*, *C. hystericina*, *C. vulpinoidea*,

and *C. lanuginosa*, but never in sufficient abundance to change markedly the floristic composition of the area. When present they are generally limited to the mesic side of the association. The more mesophytic grasses, *Calamagrostis canadensis*, *Glyceria nervata*, *Bromus ciliatus*, *Agrostis alba*, and *Phragmites communis*, occasionally change the appearance of the association late in the season owing to the height of their culms, which overtop the other species, or owing to contrast in the color of their foliage. Few species deserve to be designated as constants. *Asclepias incarnata*, *Lycopus americanus*, and *Equisetum arvense* appear in a high percentage of the stands but they may be totally absent. In late summer and early autumn *Eupatorium maculatum*, *E. perfoliatum*, *Solidago* spp., *Aster* spp., *Stachys tenuifolia*, and *Bidens frondosa* may be found in stands of considerable extent. Some of the conspicuous but ecologically unimportant species which occasionally appear are *Iris virginica*, *Symplocarpus foetidus*, *Caltha palustris*, *Lilium michiganense*, *Hemerocallis fulva*, *Spiraea alba*, and *Lobelia siphilitica*.

The composite nature of the habitat has been pointed out by Nichols (6). He mentions a few of the hydrophytic species which are able to grow in the moist substratum between the tussocks and a number of plants which are able to thrive in the drier substratum of the tussock itself. Shade tolerant species are especially characteristic of the inter-tussock vegetation. In general, species which propagate themselves mainly by vegetative means are found in the spaces between the tussocks. Typical species are *Equisetum arvense*, *Impatiens biflora*, *Marchantia polymorpha*, *Conocephalum conicum*, and *Typha latifolia*. Species which spread readily by seed commonly grow from the tops of the tussocks. *Bidens frondosa* is probably the best example, especially on tussocks growing in ponds. In early summer its seedlings may be found in the crowns of the tussocks. As the season progresses the tap roots grow down the sides of the pedestals, apparently keeping pace with the lowering water table. In well grazed pastures where *Carex stricta* persists only as a relict, *Verbena hastata* is almost invariably present in the crowns of the tussocks.

Woody forms are represented by various willows, especially *Salix discolor*, *S. petiolaris*, and *S. interior*. Occasionally *Spiraea alba*,

Cornus stolonifera, and *Rhamnus alnifolia* appear as isolated individuals in the meadow. More commonly the willows appear *en masse* at the margin of the association, where they represent the stage in succession that is to follow.

A statistical analysis of four stands is shown in table II. Stand no. 1 borders a small pond; it is about 3 acres in extent. Stand no. 2 covers the floodplain of a small stream, the ground sloping gradually upward on either side of the stream; it covers an area of approximately 15 acres. Stand no. 3 lies in a drained depression of the Kettle Moraine; it has an area of 4 acres. Stand no. 4 lies on an east facing slope characterized by seepage and underground springs; it occupies about three-fourths of an acre.

In table II the numbers or symbols in the columns have the following significance: constancy is indicated by the number preceding each period; vegetational cover is indicated by the number following. Species of infrequent occurrence are represented by a plus sign. When the species is absent from the stand this is indicated by a minus sign. Presence and cover are expressed in five degrees as follows (1):

Presence:

1, present in less than $\frac{1}{5}$ of quadrats studied
2, present in $\frac{1}{5}$ to $\frac{2}{5}$ of quadrats studied
3, present in $\frac{2}{5}$ to $\frac{3}{5}$ of quadrats studied
4, present in $\frac{3}{5}$ to $\frac{4}{5}$ of quadrats studied
5, present in $\frac{4}{5}$ to $\frac{5}{5}$ of quadrats studied

Cover:

1, covering feeble, less than $\frac{1}{20}$ of area
2, covering $\frac{1}{20}$ to $\frac{1}{4}$ of area
3, covering $\frac{1}{4}$ to $\frac{1}{2}$ of area
4, covering $\frac{1}{2}$ to $\frac{3}{4}$ of area
5, covering more than $\frac{3}{4}$ of area

COMPETITION AND ADAPTATION WITHIN THE ASSOCIATION.—A plant association may be more than a collection of species adapted in the same or in different fashion to similar conditions of habitat (9). It may include species which are not adapted and species which are so aggressive or capable of occupying the area that their presence

TABLE II

TUSSOCK ASSOCIATIONS

NUMBER OF STAND	1	2	3	4
SIZE OF QUADRAT	1 SQ. M.	1 SQ. M.	1 SQ. M.	1 SQ. M.
QUADRATS SCORED	12	20	18	24
VEGETATION COVER %	70	100	100	100
TYPE OF HABITAT	BORDER OF POND	FLOOD-PLAIN	DEPRES-SION	HILLSIDE (SPRINGS)
Carex stricta	5 . 3	5 . 5	5 . 5	5 . 5
Solidago spp.	1 . 1	3 . 2	3 . 1	1 . 1
Equisetum arvense	+	2 . 1	3 . 1	—
Impatiens biflora	2 . 1	1 . 1	1 . 1	1 . 1
Eupatorium maculatum	+	2 . 2	1 . 1	+
E. perfoliatum	+	2 . 2	+	+
Asclepias incarnata	1 . 1	2 . 1	+	—
Bidens frondosa	3 . 2	—	—	—
Galium asprellum	—	3 . 2	—	—
Typha latifolia	—	1 . 1	—	—
Salix petiolaris	1 . 1	1 . 1	—	—
S. interior	1 . 1	—	—	—
S. bebbiana	1 . 1	—	—	—
Caltha palustris	1 . 1	+	+	—
Iris virginica	1 . 1	—	—	—
Scirpus palustris	1 . 1	—	—	—
Rumex verticillatus	+	+	1 . 1	—
Stachys tenuifolia	—	+	2 . 2	—
Ambrosia artaemisiifolia	—	—	1 . 1	—
Viola sp.	—	1 . 1	—	—
Calamagrostis canadensis	—	—	1 . 1	—
Marchantia polymorpha	—	1 . 2	—	—
Conocephalum conicum	—	—	—	1 . 1
Barbula unguiculata	—	1 . 1	—	—
Symplocarpus foetidus	—	—	—	1 . 3
Hemerocallis fulva	—	+	—	—
Lilium michiganense	—	+	—	—
Smilacina stellata	—	—	—	1 . 1
Carex lanuginosa	—	1 . 1	—	—
Thalictrum dasycarpum	—	1 . 1	—	—
Spiraea alba	—	+	—	—
Verbena hastata	—	—	—	1 . 1
Campanula aparinoides	—	1 . 1	—	—
Aster novae-angliae	—	1 . 1	—	—
Lycopus americanus	—	2 . 1	1 . 1	—
Carex retrorsa	+	—	—	—
Carex spp.	+	+	+	+
Lysimachia thyrsiflora	+	—	—	—
Carex riparia	1 . 1	—	—	—
Trifolium procumbens	—	—	+	—
Solanum dulcamara	—	—	—	+
Chelone glabra	—	+	—	—
Lobelia siphilitica	—	—	—	+
Helianthus grosseserratus	—	+	—	—

is detrimental to the characteristic species. SHERFF (8) has emphasized two types of relationships which may exist within a community: the complementary, in which the plant organs grow and vegetate at different levels; and the competitive, in which the plant members occupy the same stratum. These relationships will be considered now from the standpoint of the aerial and of the subterranean plant organs.

AERIAL RELATIONSHIPS.—Among the complementary species of the association are those plants which show a marked seasonal adaptation. An examination of the tussock meadow in early spring shows a number of species which flower and fruit long before the dense growth of sedges has formed a closed cover. There are many shallow-rooting species present which become inconspicuous or disappear entirely with the advent of summer. All of these grow in the spaces between the tussocks where there is an abundance of moisture and light during the early growing season. By June 15 they are usually overtopped by the sedges.

In late summer and early autumn a considerable number of species appear which exceed the general meadow cover in height but which may be still considered mostly complementary in their aerial relationships. The period of flowering and fruiting comes after the typical meadow vegetation has ceased to grow vigorously or has even become dry. *Eupatorium purpureum*, *Solidago serotina*, *Helenium autumnale*, and *Aster novae-angliae* may be placed in this group.

Stratification is not especially marked in the tussock meadow, although a number of species present show a definite light or moisture requirement. Data obtained from atmometer studies (see later paragraphs) in these meadows conform to the findings of YAPP (15) that the evaporation rate rapidly increases from the ground upward. There is little doubt that the presence of mosses and liverworts at the lowest level may be correlated with the abundance of moisture, the higher humidity, and the dense shade. Among the species which grow in the shade of the tussock sedge are *Impatiens biflora*, *Ambrosia artemisiifolia*, *Equisetum arvense*, *Dryopteris thelypteris*, *Trifolium procumbens*, *Pilea pumila*, and seedlings of

Xanthium sp. Owing to their relatively weak growth, none of these may be considered as aerial competitors of the sedge.

Among the competitive species of greatest importance are those which grow concurrently with the dominant vegetation. Most of the sedges and grasses of the association belong to this group. Of these, *Calamagrostis canadensis* is probably the most important. In the drier portions of a tussock meadow the culms of this grass may occasionally equal or exceed in number those of *Carex stricta*. In late summer the grass gains the ascendancy over the sedge and may even obscure the latter in dense stands. In the moister areas, however, *Calamagrostis* loses its aggressiveness and appears only in scattered bunches, if it is present at all. Of lesser importance are the sedges, *Carex vulpinoidea*, *C. hystericina*, *C. lanuginosa*, and *C. stipata*, and the grasses *Phragmites communis*, *Bromus ciliatus*, *Spartina pectinata*, *Leersia oryzoides*, and *Glyceria nervata*. Other species such as *Scirpus atrovirens* and *S. lineatus* are of such infrequent occurrence that they are of little importance as competitors.

A number of species which may be considered as strongly competitive are those which commonly grow on the tops of the tussocks. Drude (**2**) states in his description of *Carex stricta* meadows in Hungary that a motley array of plants establish themselves on the tops of the tussocks even when they are still in ponds. However, he mentions specifically only the thistles and orchids. Nichols (**6**) mentions a number of plants that grow on the tussocks in Connecticut swamps. In general, plants which reproduce by seeds appear to be the most frequent invaders of the tussocks themselves. At best these intruders find themselves in uncongenial surroundings. They have to contend with the overwhelming numbers of sedge leaves; their roots must penetrate a tangled substratum of dead culms, rhizomes, and matted rootlets; and not infrequently the top of the tussock dries out before the young seedlings have established themselves.

One of the most successful of these invaders is *Bidens frondosa*. It begins its growth in the middle of summer and attains its greatest luxuriance long after the sedges have reached their maturity. It reaches its greatest abundance in areas which are shaded by taller

species, particularly the willows. Its presence in such situations is a good indication that the tussock association is disappearing.

SUBTERRANEAN RELATIONSHIPS.—An examination of the root system of *Carex stricta* reveals the fact that the greatest competition in the tussock meadow is not above but below the surface of the soil. It explains to a certain extent the ability of the tussock sedge to occupy the habitat almost to the exclusion of everything else. Aided by its aerating system, the sedge permeates the saturated soil with roots and rhizomes. The interrelationships of the subterranean organs of the tussock sedge with other species and their possible significance will be considered now.

SAGITTARIA.—This plant, particularly in ponds being invaded by *Carex stricta*, frequently forms a border on the hydric side of the tussock association. It almost never mingles with the tussocks. The transition from the *Sagittaria* zone to tussock meadow is abrupt. SHERFF (8) has pointed out that the habit of growth of *Sagittaria* does not favor a compact grouping of individuals, since the rhizomes are not of the mat producing type. It can be invaded easily by *C. stricta*. On the other hand, although rhizomes of *Sagittaria* grow to a depth of 15 cm., they cannot grow beneath the deeper root system of the sedge. Thus it appears that the sedge is limited in its advance on the pond not by the zone of *Sagittaria* but by its own ability to grow in deep water.

SPARGANIUM AND TYPHA.—These frequently border the tussock association on the hydric side, especially along streams and occasionally in ponds. Relict stands of *Typha* are sometimes found in the midst of an otherwise well developed tussock meadow. Root and rhizome competition is always marked between these species. The densely matting rhizomes of both genera are instrumental in maintaining almost pure stands, once they have become established. In addition, their compact habit of growth excludes *Carex stricta*, until the building up of soil and the consequent lowering of the water table so modify habitat conditions that the aggressiveness of *Sparganium* and *Typha* disappears.

CAREX RIPARIA.—Dense stands of this rank growing sedge are sometimes found in the tussock association, although they are not a part of it. These stands may occur on the hydric side, the mesic

side (as islands within the association), or as broad bands running completely through the association. Superficial examination discloses no very great variation in the habitat. The area occupied by *Carex riparia* apparently should support a luxuriant tussock meadow. The explanation rests upon a number of factors.

The rootstocks of *C. riparia* are very coarse and are capable of rapid growth. From the base of the culm they grow downward, and at a depth varying from 5 to 20 cm. they assume a horizontal direction for a distance of 10 to 50 cm.; the tips then grow vertically to give rise to a new plant at the surface of the ground. Roots are produced both from the base of the culm and from the nodes of the rootstock. Thus the entire soil layer to a depth of 15–20 cm. is permeated with a coarse mat of subterranean organs. Growth of the rhizomes is very rapid in the loose spongy soil.

The areas occupied by *C. riparia* are almost invariably flooded by débris and soil washed from surrounding uplands. The accumulated soil may amount to 6 inches or more within a single season. Owing to the rapid growth of rhizomes, *C. riparia* keeps pace with the rising soil level with ease. The culms are numerous, 150 or more per square meter, and because of their rank growth tend to overshadow all other plants in the same area. Hence this species occupies space to the exclusion of everything else. Under these conditions the slower growing *C. stricta* is soon covered with soil and the invasion of *C. riparia* is quickly accomplished.

Species with shallow root systems.—Throughout the association are numerous species which produce roots at or near the surface of the soil. In relation to the tussock sedge they are entirely complementary. In ponds the runners of *Ranunculus delphinifolius* frequently cover the soil surface following recession of the water (fig. 1). In the more elevated portions of the association *Asclepias incarnata*, *Penthorum sedoides*, *Echinochloa crusgalli*, *Lycopus americanus*, and *Galium* sp. may occur. They seem to offer little competition to the tussock sedge.

List of species.—The species found to occur in quadrats studied in the tussock association of the five counties previously mentioned are enumerated in the following list. The numbers preceding the species indicate their usual position in the association as follows:

(1) on the hydric side, (2) in the region of maximum development, and (3) on the mesic side or in transition areas. In general the nomenclature follows that of GRAY'S manual (7); recent changes and segregations in certain genera, however, have been observed.

Species occurring in tussock association

Musci
- (2) Barbula unguiculata (Huds.) Hedw.
- (2) Brachythecium rivulare B. & S.
- (1) Drepanocladus aduncus pseudofluitans Sanio
- (3) Bryum sp.

Hepaticae
- (1, 2) Marchantia polymorpha L.
- (1, 2) Conocephalum conicum (L.) Dum.

Polypodiaceae
- (3) Dryopteris thelypteris (L.) Gray

Equisetaceae
- (2, 3) Equisetum arvense L.

Typhaceae
- (1, 2) Typha latifolia L.

Sparganiaceae
- (1) Sparganium eurycarpum Engelm.

Alismaceae
- (1) Sagittaria latifolia Willd.
- (1) Alisma plantago-aquatica L.

Gramineae
- (3) Echinochloa crusgalli (L.) Beauv.
- (3) Zizania aquatica L.
- (3) Leersia oryzoides (L.) Sw.
- (3) Phalaris arundinacea L.
- (3) Muhlenbergia racemosa (Michx.) B.S.P.
- (3) Phleum pratense L.
- (3) Agrostis alba L.
- (2, 3) Calamagrostis canadensis (Michx.) Beauv.
- (3) C. neglecta (Ehrh.) Gaertn.
- (3) Koeleria cristata Pers.

(3) Spartina pectinata Link (S. michauxiana Hitchc.)
(1) Phragmites communis Trin.
(3) Poa pratensis L.
(1) Glyceria nervata (Willd.) Trin.
(2, 3) Bromus ciliatus L.
(3) Hordeum jubatum L.
(3) Elymus canadensis L.

Cyperaceae

(3) Eleocharis obtusa (Willd.) Schultes
(1, 2, 3) E. palustris (L.) R. & S.
(3) E. acicularis (L.) R. & S.
(1) Scirpus fluviatilis Gray
(3) S. atrovirens Muhl.
(3) S. lineatus Michx.
(3) Carex bebbii Olney
(3) C. sterilis Willd.
(3) C. bromoides Schkuhr.
(3) C. vulpinoidea Michx.
(3) C. stipata Muhl.
(3) C. sartwellii Dewey
C. stricta Lam.
(3) C. strictior Dewey
(3) C. pennsylvanica Lam.
(2, 3) C. lanuginosa Michx.
(3) C. trichocarpa Muhl.
(1, 2, 3) C. riparia W. Curtis
(3) C. hystericina Muhl.
(1) C. retrorsa Schw.
(2, 3) C. rostrata Stokes

Araceae

(2) Symplocarpus foetidus (L.) Nutt.

Lemnaceae

(1) Lemna trisculca L.

Juncaceae

(3) Juncus tenuis Willd.
(3) J. dudleyi Wieg.

Liliaceae
(2) Hemerocallis fulva L.
(3) Lilium michiganense Farwell
(2) Smilacina stellata (L.) Desf.

Iridaceae
(1) Iris virginica L.
(3) Sisyrinchium gramineum Curtis

Salicaceae
(3) Salix nigra Marsh.
(1, 2, 3) S. amygdaloides Anders.
(1) S. lucida Muhl.
(1, 2, 3) S. interior Rowlee (S. longifolia Muhl.)
(1, 2, 3) S. cordata Muhl.
(1, 2, 3) S. discolor Muhl.
(1, 2, 3) S. petiolaris Smith
(1, 2, 3) S. bebbiana Sarg. (S. rostrata Richards)
(2) S. candida Flügge

Urticaceae
(3) Urtica procera Muhl. (U. gracilis American authors)
(3) Laportea canadensis (L.) Gaud.
(2) Pilea pumila (L.) Gray
(3) Boehmeria cylindrica (L.) Sw.

Polygonaceae
(3) Rumex crispus L.
(2, 3) R. verticillatus L.
(1) Polygonum sp.

Ranunculaceae
(1) Ranunculus delphinifolius Torr.
(3) R. abortivus L.
(2) R. pennsylvanicus L.f.
(2, 3) Thalictrum dasycarpum Fich. & Lall.
(3) Anemone virginiana L.
(3) A. canadensis L.
(1, 2) Caltha palustris L.

Cruciferae
(3) Cardamine bulbosa (Schreb.) B.S.P.
(3) C. douglassii (Torr.) Britton

Crassulaceae
(3) Penthorum sedoides L.
Saxifragaceae
(3) Saxifraga pennsylvanica L.
(3) Parnassia caroliniana Michx.
Rosaceae
(2) Spiraea alba DuRoi
(3) Potentilla monspeliensis L.
(2, 3) Rosa carolina L.
Leguminosae
(2) Trifolium procumbens L.
(3) Lathyrus palustris L.
(3) Apios tuberosa Moench.
Callitrichaceae
(1) Callitriche palustris L.
Balsaminaceae
(1, 2, 3) Impatiens biflora Walt.
Rhamnaceae
(2) Rhamnus alnifolia L'Her.
Violaceae
(2, 3) Viola cucullata Ait.
(2) V. blanda Willd.
Onagraceae
(2) Epilobium densum Raf.
Umbelliferae
(1) Cicuta maculata L.
(1) Sium suave Walt. (S. cicutaefolium Schrank.)
(3) Zizia aurea (L.) Koch
(2) Pastinaca sativa L.
(3) Oxypolis rigidior (L.) Coult. & Rose
(3) Angelica atropurpurea L.
Primulaceae
(1) Lysimachia thyrsiflora L.
Gentianaceae
(3) Gentiana andrewsii Griseb.
Asclepiadaceae
(1, 2) Asclepias incarnata L.
(3) A. syriaca L.

Verbenaceae
(3) Verbena hastata L.
Labiatae
(1) Scutellaria lateriflora L.
(1) S. galericulata L.
(3) Prunella vulgaris L.
(2) Physostegia virginiana (L.) Benth.
(3) Stachys tenuifolia var. aspera (Michx.) Fernald
(2, 3) Lycopus virginicus L.
(2, 3) L. americanus Muhl.
(3) Mentha arvensis var. canadensis (L.) Briquet
Solanaceae
(3) Solanum dulcamara L.
Scrophulariaceae
(3) Linaria vulgaris Hill.
(3) Scrophularia marilandica L.
(2) Chelone glabra var. linifolia Coleman
(3) Mimulus ringens L.
Plantaginaceae
(3) Plantago major L.
Rubiaceae
(2) Galium asprellum Michx.
Campanulaceae
(2, 3) Campanula aparinoides Pursh
Lobeliaceae
(2, 3) Lobelia syphilitica L.
Compositae
(2, 3) Eupatorium purpureum L.
(2, 3) E. perfoliatum L.
(3) Solidago canadensis L.
(3) S. serotina Ait.
(2, 3) Aster novae-angliae L.
(2, 3) A. puniceus L.
(3) Ambrosia artemisiifolia L.
(3) Xanthium sp.
(3) Rudbeckia hirta L.
(3) Helianthus grosseserratus Martens

(1) Bidens frondosa L.
(3) B. connata Muhl.
(3) Helenium autumnale L.
(3) Cirsium lanceolatum (L.) Hill

Succession

The tussock meadows in these areas constitute a stage in succession which is usually preceded by a reed-swamp stage and followed by the *Eleocharis-Juncus-Carex* complex of the typical hydrosere. The limits of the sedge meadow are usually well marked, owing to the growth form of its principal species, *Carex stricta*. The transition from open water (fig. 4) or from the reed-swamp stage to the tussock meadow is usually abrupt. Telescoping is occasionally apparent if the habitat conditions are changing rapidly or the topography is variable within the area. The tension zone along streams may be even more marked if the land rises gradually on both sides of the stream. In flat areas the association may be uniform throughout, although islands of relicts from preceding stages or of invaders indicating the stages to follow are occasionally present.

The transition to the following stage is usually a gradual one and is indicated more by the decreasing numbers of the tussocks than by the appearance of new or otherwise conspicuous species. The outer limits of the association are especially well marked in areas where rising ground is accompanied by a rapid increase in depth of the water table, in situations marked by abrupt changes in the soil type, and in grazed areas. Heavy pasturage may result in grassland directly bordering the tussock meadow. In all cases the boundary of the association may be determined by the presence or absence of the tussock sedge.

The *Eleocharis-Juncus-Carex* complex which usually succeeds the tussock association is dominantly herbaceous. The most characteristic species are *Eleocharis palustris*, *Juncus dudleyi*, and *Carex bebbii*. The less frequent *Scirpus atrovirens* is usually present and is rendered conspicuous by its coarser growth and greater height. Intermingled with these species are various sedges and grasses: *Carex vulpinoidea*, *C. sartwellii*, *C. hystericina*, *Bromus ciliatus*, *Leersia*

oryzoides, *Glyceria nervata*, and *Calamagrostis canadensis*. A considerable array of dicotyledonous forms appears throughout the season. If the area is not subjected to heavy grazing, *Rumex crispus*, *Ranunculus abortivus*, *Penthorum sedoides*, *Saxifaga pennsylvanica*, *Lathyrus palustris*, *Mentha arvensis*, *Lycopus americanus*, *Mimulus ringens*, and *Lobelia syphilitica* are usually present. The autumnal aspect is usually characterized by a display of *Aster* and *Solidago* spp. which may completely obscure the meadow-like appearance of the complex.

In the tension zone between the tussock association and the *Eleocharis-Juncus-Carex* complex, *Carex stricta* usually shows a definite change in growth form. The pedestals become low mounds or merely tufts of culms growing at the soil level. Occasionally the spaces between the tufts become occupied by culms that have grown from rhizomes and a uniform distribution results. At this stage the tussock sedge is sometimes difficult to distinguish from the closely related *C. strictior*, which grows in mats rather than in tussocks. The deep green leaves of the former, however, serve to distinguish it from the paler glaucous foliage of the latter. By digging up the root system of *Carex stricta* in such places the remains of buried tussocks can sometimes be found.

In areas not subjected to grazing, succession may proceed through a shrub stage to a swamp forest. In such cases the most successful invaders of the tussock association are the willows and *Cornus stolonifera*. The shrubby willows, *Salix interior*, *S. petiolaris*, *S. discolor*, *S. lucida*, *S. bebbiana*, and *S. cordata*, are more aggressive than the tree willows, *S. amygdaloides* and *S. nigra*. All may be found in a single willow thicket bordering the tussock meadow or invading it from the pond side.

The willow stage is usually succeeded by a tree stage characterized by *Fraxinus nigra*, *F. americana*, *Quercus bicolor*, *Ulmus fulva*, and *Acer rubrum*. The shrubs *Alnus* sp., *Ribes grossularia*, *Cornus stolonifera*, *Sambucus canadensis*, and *Xanthoxylum americanum*, and the liana *Psedera quinquefolia* are frequent. The herbaceous layer may consist principally of sedges and grasses if the forest is open. In the shaded areas *Boehmeria cylindrica*, *Pilea pumila*, *Parietaria pennsylvanica*, *Laportea canadensis*, *Eupatorium purpureum*, and

Lycopus americanus are common. In open spaces in these forests tussocks sometimes persist.

In heavily grazed areas the *Eleocharis-Juncus-Carex* complex is generally absent. Bluegrass pasture directly borders the tussock association. The coarser culms of the sedge are apparently unpalatable to livestock, since the grass is eaten down to the bare earth before the sedges are touched. Occasionally the marginal tussocks around ponds are killed by livestock and remain as low, grass covered mounds. This has led to a generally accepted opinion among farmers that tussock meadows result from the trampling of cattle. The best development of the tussock meadow, however, appears in areas where domestic animals are never permitted, especially along railroad rights of way.

Environmental factors within the association

Evaporation

During the summer of 1929 atmometer studies were made in the area south of Cedarburg. Stations were established as follows: (1) in the flat tussock meadow, (2) in the hillside tussock meadow (on an east facing slope), (3) in the *Eleocharis-Juncus-Carex* complex, and (4) in the adjoining grassland. The atmometers were run in triplicate, with one bulb placed at 20 cm., one at 50 cm., and one at 120 cm. above the ground. In every case the third bulb was well above the level of the vegetation. The results are summarized in table III.

It is evident from the data obtained that evaporation above the vegetation varies little in rate over the entire area. The rates recorded are probably higher than the average, owing to the continued drought of that year. In a nearby beech-maple forest at a height of 20 cm. the evaporation rate varied from 6 to 14 cc. per day for the same period. The only effect of the drought on *Carex stricta* that was observed was the folding of the leaves on dry hot days. Long after the grassland had dried up and turned brown, the tussock meadow was still green and luxuriant.

The slight evaporation in the lower levels of the tussock meadow accounts for the persistence of many of the shade loving herbaceous

forms. Supplied with an abundance of moisture for their roots and subject to the greater humidity beneath the sedge cover, they were little affected by the drought. It was to be expected that evaporation near the ground would be influenced by the density and structure of the vegetation. In passing from station 1 to station 4 the increasing evaporation rate in the lower levels is well shown in table III. Correlated with this is the increasing openness of the stand and

TABLE III

AVERAGE DAILY EVAPORATION RATES (IN CC.) AT DIFFERENT LEVELS IN TUSSOCK MEADOWS AND ADJACENT ASSOCIATIONS

STATIONS	HEIGHT OF ATMOMETER BULBS		
	20 CM.	50 CM.	120 CM.
(1) Flat tussock meadow	9.1	21.2	38.1
(2) Hillside tussock meadow	11.3	24.6	39.0
(3) Eleocharis-Juncus-Carex complex	18.2	32.4	42.8
(4) Grassland	36.1	43.4	44.9

the decreasing evidence of stratification. The stratification that is evident in many tussock meadows is due in great part, as YAPP (15) has shown for other meadows, to variations in the rate of evaporation at different levels. The obvious conclusion is that evaporation plays little part in determining where a tussock meadow will grow, but that it must be considered a factor which helps determine the floristic composition of the meadow.

SOIL

The soil in these areas is usually a clay or silt loam. The surface layer of 12 to 15 inches is a black compact loam, rich in organic matter. Occasionally it is peaty in nature or shows a fibrous condition as a result of its plant remains. The color is brown or black, depending upon the degree of decomposition. The texture may vary according to the amount of material washed in from the surrounding uplands. The surface layer may be underlain by grayish or fine white sand, or occasionally by a zone of calcareous pebbles. The subsoil is a bluish silty clay which extends downward for several feet.

The surface of these areas is level or it slopes very gradually toward the adjoining drainage courses. Drainage is deficient, the surface water frequently standing for some time in the spring. Areas occurring along stream courses may be subject to overflow. Since the soil of the region is mainly derived from the Niagara limestone, the soils of the tussock meadows are alkaline, owing to the percolation of lime-containing water from the adjacent uplands.

Soil reaction.—More than 200 tests were made in the tussock meadows of Washington, Ozaukee, Milwaukee, and Waukesha counties. In every case the soil was found to be alkaline. The pH ranged from 7.2 to 8.1, with an average of 7.4. The lower soil horizons tended to be slightly more alkaline than the surface layer. The water of ponds and small streams showed approximately pH 8. No difference was noted between the soil reaction at the bases of tussocks and that in the tussocks themselves.

Although the soil of tussock meadows in the area studied was consistently alkaline, pH does not appear to be a limiting factor. Several tussocks were dug up and transplanted to the edge of Cedarburg Bog where the water is continuously acid. After two years the sedges were still growing, although subject to the competition of the bog vegetation, particularly *Phragmites communis*, *Carex filiformis*, and *Salix candida*. In the greenhouse *Carex stricta* grows luxuriantly in *Sphagnum* moss. When watered with tap water (from Lake Michigan) the moss showed a pH of 7.02. When watered with distilled water, or with water to which a slight amount of sulphuric acid had been added, the pH varied from 5.6 to 6.8. No differences in growth or color of the plants could be observed throughout this range.

Soil moisture.—The range of soil moisture in different stands of the tussock association was very great; in individual stands a marked seasonal variation was also observed. Owing to the large amount of organic matter in the spongy upper layer of the soil, the typically poor drainage, and the frequent occurrence of springs, an excess of moisture was present for a considerable part of the season. Based on the dry weight of the soil, the moisture content frequently exceeded 250 per cent. With the lowering of the water table the moisture content slowly dropped until it reached 60 to 80 per cent in late summer. In the subsoil the water content was much lower,

ranging from 20 to 60 per cent. In August, soil moisture in the *Eleocharis-Juncus-Carex* complex ranged from 40 to 60 per cent in the upper 6 inches and slightly less in the subsoil. Soil moisture was never reduced to the hygroscopic coefficient or to a point where it was unavailable for plant growth. Consequently it doubtless is never a direct limiting factor in the persistence of the tussock meadow.

Water table

A close correlation exists between the presence or absence of tussock meadows in an area and the level of the water table. In the areas of maximum development the water table stands at or near the surface throughout the season. The average depth of the water table in the low hummocky area south of Cedarburg, during the summer of 1929, was 4.8 inches. Rains frequently brought the water table to the surface but it always subsided within a few days. At no time during the entire summer did it fall below 11 inches.

The water table reaches its highest level in April and May as a result of the spring rains. At this time the water in ephemeral ponds may stand at a depth of 18 to 24 inches; in flat or gently sloping areas bordering stream courses it usually stands at the surface; on hillsides, where drainage is better, it stands a few inches below the surface. With the advance of summer it is gradually lowered until the minimum is reached in late August or early September, after which it again slowly rises.

Other workers have recognized the influence of the water level on the character of the vegetation. Warming (10) states, "In many cases ground-water lies too high for certain plants; in other cases it is so far below that the roots cannot utilize it directly or indirectly; in still other cases it is at such a depth as to be reached by the roots at certain seasons, but not at others." Stout (9) mentions, "It is universally recognized that the amount of water in a soil and the level at which the ground water stands are important direct factors in determining the character of the plant life which is present." It is possible to estimate with considerable accuracy the depth of the water table in these meadows by considering the season of the year and noting the character of the vegetation. "Islands" in the vegetation almost invariably indicate a difference in water level.

Evidence that the level of the water table has a direct influence on the character of the vegetation is furnished by drainage projects which are being carried out in some places. The placing of tile in a tussock meadow will result in the complete disappearance of the tussocks in a very few years. Measurements of the distance to the water table in such areas near Thiensville, Wisconsin, have shown that the water level is from 2 to 4 feet beneath the surface of the soil. Owners of the land thus drained state that 10 years ago the water stood at the surface for a greater part of the growing season and that well developed tussocks were present at that time.

Records of the water table in a small tussock area on a hillside south of Cedarburg were kept during the summers of 1931 and 1932. Small drainage ditches had been dug in order to make the area suitable for an apple orchard. The average level of the water table dropped approximately 6 inches a year. On September 20, 1933, the water table was 34 inches below the surface. Although the sedge vegetation was still present the area was characterized by a marked invasion of grasses, particularly *Poa pratensis*, and numerous weeds, including a few specimens of *Verbascum thapsus* and a great many *Solidago* spp. The dried stems of *Linaria canadensis* and *Prunella vulgaris* were also abundant. It is obvious that drainage is rapidly causing the disappearance of *Carex stricta* in this place.

Biotic factors

Grazing

The effect of grazing upon the tussock vegetation is noticeable only when the number of livestock present greatly exceeds the capacity of the pasture. Most of the better pasture lands are of the bluegrass type, tussock associations occasionally being present as local areas in the pasture. Pure tussock meadows are seldom used for grazing.

Most of the grazing is done by cattle and horses. Ordinarily they graze the tussocks only when the grass has been depleted. If the pasture is overstocked the complete disappearance of the tussocks may result. Around ponds the grass covered mounds, representing former tussocks, may be observed as a zone bordering those which

still remain. Where grazing is not intensive the tussocks may remain for a long time. Bluegrass invades the spaces between them and along with the grazing prevents their vegetative propagation by means of rhizomes. Under these conditions various weeds characteristically grow in the protection of the tussock crown.

Intensive grazing generally results in greater exposure of the soil and consequently in a decrease of moisture and a lowering of the

FIG. 8.—Winter aspect of tussocks with burned-over area at left; water table near surface in summer.

water table. Succession toward a bluegrass pasture is thus hastened. Succession toward the shrub and forest stages does not take place under the influence of grazing.

FIRE

Farmers commonly burn these areas each year after the vegetation has become dry (fig. 8). The opinion prevails that burning will cause the disappearance of the tussocks or improve the grazing qualities of the pasture. It does neither. Burning results in the removal of the dried leaves and culms which serve to fill in the spaces between the tussocks. The roots and rhizomes are not harmed to any great extent by fire. Burning, however, does permit an increased invasion of weeds into the area and drives out or kills the small game animals that frequent the meadow. It is a practice which might well be discontinued.

Rodents

The destruction of tussocks is sometimes hastened by rabbits and mice. When food is scarce these animals sometimes eat the exposed roots and rhizomes just beneath the tuft of dead leaves. In the region of the cut ends of these organs a constriction in the pedestal occurs. The soil surrounding the roots remaining nearest the surface may crumble as a result of frost action or be washed away by rain. Renewed attacks of the rodents may so weaken the pedestal that it topples of its own weight. The destruction of tussocks by this means, however, is negligible.

Discussion

The conditions of the habitat occupied by the tussock sedge lie within the limits of tolerance of many other species; consequently the explanation of the dominance of *Carex stricta* in the tussock association must be sought primarily in the characteristics of the plant itself. Among the characteristics of a dominant Weaver and Clements (12) include size, abundance, and duration. *Carex stricta* has all of these.

The chief competitors of the tussock sedge are species of similar form, the grasses and other sedges. Few of these are taller than *Carex stricta* and all lack the additional advantage in height contributed by a pedestal. In early spring when growth begins, the height of the pedestal represents an advantage which, under favorable conditions, is generally maintained. Thus species which grow concurrently with the tussock sedge are at a disadvantage from the beginning.

The abundance of culms is apparent even at a glance. Statistical studies show that *Carex stricta*, in areas of maximum development, may constitute almost 100 per cent of the vegetation. Abundant tillering takes place and new buds and culms may be produced throughout the summer.

The perennial nature of the tussocks and the considerable age to which they attain are factors which help to bring about their permanent occupancy of an area. The mass of dead leaves and the matted roots and rhizomes which are added to the soil each year tend to create a fibrous peat which is favorable to the continued growth of the sedge.

The cespitose habit contributes to the dominance of *Carex stricta* in still another way. It constitutes an admirable adaptation to a fluctuating water level. During that portion of the growing season when the water is well above the surface of the ground, the leaves and stems are seldom if ever submerged. Aeration of roots and rhizomes presents no problem, owing to their well developed aerenchyma. With the lowering of the water table and the consequent decrease in moisture supply in the region of the fibrous roots, the soil roots in the zone of saturation supply the necessary moisture. The demand for moisture during times of stress is lessened to some extent by the folding of the leaves.

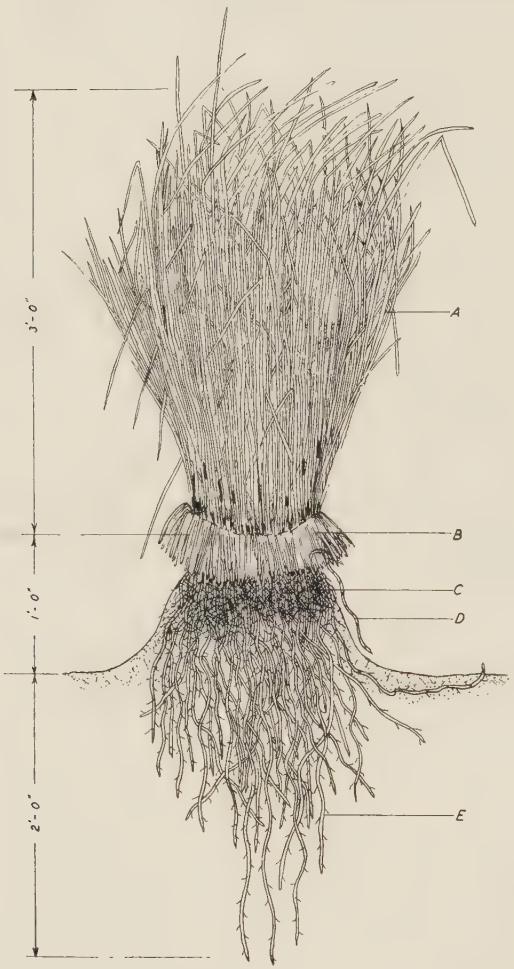


FIG. 9.—Diagrammatic sketch of a *Carex stricta* tussock: *A*, leaves of current growing season; *B*, dead leaves of previous season; *C*, fibrous roots in earthy pedestal; *D*, rhizome; *E*, wirelike soil roots.

The factors which appear most to limit the growth of the tussock sedge are deficiency of water, soil type, shade, and grazing. A water depth greater than 18–24 inches in ponds is usually not conducive to the growth of tussocks. Likewise, *Carex stricta* is seldom present in areas where the water table falls more than 18–24 inches below the surface during the growing season. The rapid disappearance of

the association following drainage is evidence in support of this view. The moisture content of the soil may also be correlated with the average depth of the water table. In well developed tussock meadows the moisture content of the soil seldom falls below 60 per cent during the growing season. In adjacent associations where *Carex stricta* is absent it may fall as low as 15 per cent during periods of drought.

Soils low in organic matter never support tussock vegetation. In fact it appears that the soil must be somewhat peaty before the tussock sedge can even invade an area. Again, a water relation may exist, since peaty soils are capable of holding a high percentage of moisture. On the other hand the tussocks do not occur on sandy substrates, especially where the drainage is good and the moisture content falls rapidly with the advance of the dry season.

The effect of shade is especially apparent when the association is being invaded by shrubs and trees. Permanent quadrats, which were observed for a period of five years under medium sized trees of *Salix amygdaloides*, *S. nigra*, and *Ulmus americana* which had become established in an otherwise pure tussock association, show the disappearance of certain of the tussocks and a gradual invasion of herbaceous dicotyledonous forms, both in the spaces between the pedestals and in the crowns of the tussocks themselves. Quadrats in areas being invaded by shrubby willows show an even faster rate of disappearance.

Among the factors of the environment which do not appear to be limiting are evaporation and soil reaction. Although the evaporation rate varies in the various levels of the association and determines to an extent the nature of the secondary vegetation, it is little different at the upper level of the tussock meadow from the rate in adjacent associations. It does not appear to be a factor in succession. Similarly the hydrogen ion concentration of the soil in the different soil horizons and in the associations preceding and following the tussock association appears to remain fairly constant. Variations that occur are not large enough to be significant.

The omission of the tussock association in certain successions seems worthy of note. This is especially true of lakes with sandy shores and the margins of quaking bogs. In many of these areas the

proper soil is lacking although the water content may be high. Although *Carex stricta* has been grown in sand in the greenhouse, with difficulty, its ability to compete with sand-loving species in nature is doubtful. It is probable that this species has been excluded from the margins of many lakes as a result of its inability to migrate. Although the seeds are easily carried they have not been observed to germinate in nature, and all attempts to germinate them in the laboratory have failed. In addition, a surprisingly small number of fruiting plants have been found in the region studied.

The rapid succession that takes place around many lakes is also a factor which serves to exclude the slowly developing tussock sedge. In many instances the shrub stages are found at the very margins of lakes. In such cases light enters immediately as a limiting factor. Similarly the shrub stages in bogs may encroach rapidly upon the sedge vegetation, working destruction on species that depend more upon permanent establishment than upon migratory ability for their existence. The unstable substratum of the floating mat is also a poor foundation for a plant which needs firm anchorage for its pedestals. The effect of physiological conditions in bogs upon *Carex stricta* cannot be stated. Tussocks transplanted to bogs, however, have grown with a moderate degree of success for a period of two years.

Summary

1. The vegetation and environmental conditions of tussock meadows in southeastern Wisconsin were studied during the summers of 1929, 1932, and 1933.

2. Tussock meadows are developed along stream and pond margins, on springy hillsides, and in drained morainic depressions. They are found on soils showing a high percentage of organic matter.

3. Tussock meadows are dominated by a single species, *Carex stricta*, which produces tussocks that consist of a tuft of leaves and culms at the summit of a pedestal composed of roots, rhizomes, soil, and vegetable débris.

4. New tussocks are initiated by means of rhizomes which grow horizontally from the bases of old tussocks.

5. Individual tussocks may attain a height of 2 to 4 feet and a diameter of 8 to 30 inches. They may persist in an area for many years.

6. The leaves of *Carex stricta* show certain xeromorphic structures which indicate an adaptation to the excessive evaporation rates to which they are occasionally subjected. The roots and rhizomes show hydromorphic structures which indicate an adaptation to extremely moist conditions.

7. The tussock habit enables *Carex stricta* to persist in areas where the water level shows a marked seasonal fluctuation.

8. The tussock association is almost exclusively herbaceous. The most important secondary species are grasses and sedges. Dicotyledonous herbs may dominate in appearance but not in numbers at certain seasons.

9. *Carex stricta* furnishes marked competition for herbaceous species from the standpoint of both aerial and subterranean organs.

10. Progressive decrease in soil moisture and lowering of the water table lead to invasion by species of lower moisture requirements and the ultimate disappearance of the tussock association.

11. In succession, the tussock association is usually preceded by a reed-swamp stage and followed by a sedge-rush stage. The association may be invaded by willows which are eventually succeeded by a swamp forest.

12. Evaporation, annual fires, and soil reaction are not significant factors in succession.

13. Overgrazing may result in the disappearance of the tussock association and the appearance of grassland in its place.

The writer expresses his appreciation to Professor GEORGE D. FULLER of the Department of Botany of the University of Chicago for helpful suggestions and criticisms during the progress of this investigation.

ROCKY MT. FOREST AND RANGE EXPERIMENT STATION
FORT COLLINS, COLORADO

LITERATURE CITED

1. BRAUN-BLANQUET, J., and PAVILLARD, J., Vocabulaire de sociologie végétale. Montpellier. 1925.
2. DRUDE, O., Handbuch der Pflanzengeographie. pp. 292–294. Stuttgart. 1890.
3. HAYDEN, A., The ecologic subterranean anatomy of some plants of a prairie province in central Iowa. Amer. Jour. Bot. 6:87–105. 1919.

4. MACKENZIE, K. K., Notes on *Carex*. VIII. *Carex stricta* Lam. and its allies. Bull. Torr. Bot. Club **42**:405–422. 1915.
5. MARTIN, LAWRENCE, The physical geography of Wisconsin (2nd ed.). pp. 226–231. Bull. 36. Ed. Series no. 4. Wisconsin Geol. and Nat. Hist. Surv. Madison. 1932.
6. NICHOLS, G. E., The vegetation of Connecticut. IV. Plant societies in lowlands. Bull. Torr. Bot. Club **42**:169–217. 1915.
7. ROBINSON, B. L., and FERNALD, M. L., GRAY'S New manual of botany. 7th ed. New York. 1908.
8. SHERFF, E. E., Vegetation of Skokie marsh. Bull. Illinois State Lab. Nat. Hist. **9**:575–614. 1913.
9. STOUT, A. B., A biological and statistical analysis of the vegetation of a typical wild hay meadow. Trans. Wisconsin Acad. Sci., Arts and Letters **17**:405–469. 1912.
10. WARMING, E., Oecology of plants. p. 45. Oxford. 1909.
11. WARMING, E., and GRAEBNER, P., Lehrbuch der ökologischen Pflanzengeographie. pp. 783–787. Berlin. 1930–1933.
12. WEAVER, J. E., and CLEMENTS, F. E., Plant ecology. p. 135. New York. 1929.
13. WEAVER, J. E., and FITZPATRICK, T. J., Ecology and relative importance of the dominants of tall-grass prairie. BOT. GAZ. **93**:113–150. 1932.
14. WHITBECK, R. H., The geography and economic development of southeastern Wisconsin. p. 16. Bull. 58. Ed. series no. 6. Wisconsin Geol. and Nat. Hist. Surv. Madison. 1921.
15. YAPP, R. H., On stratification in the vegetation of a marsh, and its relations to evaporation and temperature. Ann. Bot. **12**:275–319. 1909.